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AUTHOR(S):

UEHARA, Shigeo

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POPULATION DENSITIES OF DIURNAL MAMMALS SYMPATRIC WITH THE CHIMPANZEES OF THE MAHALE MOUNTAINS, TANZANIA: COMPARISON BETWEEN THE CENSUS DATA OF 1996 AND 2000

Shigeo UEHARA
Department of Ecology and Social Behavior,
Primate Research Institute, Kyoto University

ABSTRACT A route census was carried out by one observer using the same methods along the same survey routes during the same seasons in 1996 and 2000 to estimate the abundance of medium- and large-sized diurnal mammals within the home range of the chimpanzees of M Group in the Mahale Mountains, western Tanzania. All eight mammalian species censused were known to have been consumed by chimpanzees, and there are other resident predators such as leopards and crowned hawk eagles. No statistically significant differences were found in group densities of gregarious species or individual densities of non-gregarious species between the two data sets. However, frequencies of encounter with and estimates of group size of some species suggested possible decrease (bushbucks) or increase/non-decrease (red-tailed monkeys, yellow baboons, red colobus, warthogs, blue duikers and forest squirrels) from 1996 to 2000, although such an assumption could not be made for blue monkeys due to their low densities in both years. No quantitative predation data for the relevant period exist, but the results show that predation pressure as a whole including hunts by chimpanzees did not seem to exceed population growth rates of the prey mammals, with the exclusion of blue monkeys and the possible exception of bushbucks, during the 1996-2000 period at Mahale.

Key Words: Mahale Mountains; Route census; Diurnal mammals; Density; Secondary succession.

INTRODUCTION

Chimpanzees (*Pan troglodytes*) at Mahale, western Tanzania, have been intensively studied since 1965 (Nishida, 1990). Although Mahale became the 11th national park of Tanzania in 1985, information concerning other fauna and flora in the park is still insufficient. At Mahale, chimpanzee predator-mammalian prey interactions have been studied either directly (Huffman & Kalunde, 1993; Hosaka, 1995; Hosaka *et al.*, 2001; Boesch *et al.*, 2002) or indirectly (Nishida *et al.*, 1979; Kawanaka, 1982; Hasegawa *et al.*, 1983; Norikoshi, 1983; Takahata *et al.*, 1984; Uehara *et al.*, 1992; Hosaka *et al.*, 2001). Other large animals such as leopards (*Panthera pardus*) and crowned hawk-eagles (*Stephanoaetus coronatus*) are also present at Mahale as resident predators (Itani, 1977; Nishida, 1990), although quantitative data on their hunting behavior have never been collected. Continuous monitoring of changes in abundance of poten-

tial prey mammal species is important in order to understand predator-prey relationships in general over a long-term basis. Such basic data are also useful for park management planning as well as for understanding the Mahale ecosystem.

Long-term data on the fluctuation of prey mammal populations consumed by chimpanzees have not been published for any study site across Africa except for those from Gombe National Park, Tanzania and Kibale National Park (Ngogo), Uganda. It has become evident that red colobus (*Procolobus badius*) (Stanford, 1995, 1998; Mitani *et al.*, 2000) is the most frequently killed prey species at every study site where the two species are sympatric (Uehara, 1997). The purpose of this report is to present data of the route census conducted in 2000 on medium- and large-sized diurnal mammals including four species of monkeys at Mahale. Comparisons are made between the two data sets collected by the author using the same methods along the same census routes during the same seasons in 1996 and 2000.

This is the first diachronic comparison of quantitative data on population densities of diurnal mammals known to have been preyed upon at least once since 1965 by the chimpanzees of M Group. They must also have been consumed by other predators. The wild animal populations in general appeared to have gradually increased from the 1970s onward until 1996 within the home range of M Group chimpanzees (Uehara & Ihobe, 1998). Based on the hunting data collected between 1981-1990 (Uehara *et al.*, 1992) and 1991-1995 (Hosaka *et al.*, 2001) and the census data between 1995-1996 (Uehara & Ihobe, 1998), Ihobe and Uehara (1999) estimated that the chimpanzee predation rates did not exceed the population growth rates of the respective prey species (see Boesch *et al.*, 2002 for revised predation rates). If the population densities of the prey mammals censused again in 2000 show no decrease, we may conclude that predation pressure as a whole at Mahale after 1995 did not exceed the population growth rates of the prey mammals, although no quantitative predation data for the relevant period are available at the moment.

METHODS

Routes CR2 and CR3 were censused in both 1996 and 2000 (Fig. 1). Route CR1 was originally censused in 1996, but dropped in 2000 due to insufficient time in the field. Based on vegetation types along the census routes, i.e., forest (F) or woodland (W), each route was divided into two census subunits in 1996 (Uehara & Ihobe, 1998). Vegetation was checked again in 2000, but no conspicuous succession was visually recognized. CR2 (9090 m in length) consists of 6950 m of forest (F2: 76%) and 2140 m of woodland (W2: 24%), while CR3 (10861 m) consists of 4730 m of forest (F3: 44%) and 6131 m of woodland (W3: 56%) (Uehara & Ihobe, 1998: Table 1). Forest occupies 59% of the length of the two routes censused in 2000 (Fig. 1).

The subject species were the same as those censused in 1996, i.e., red-tailed

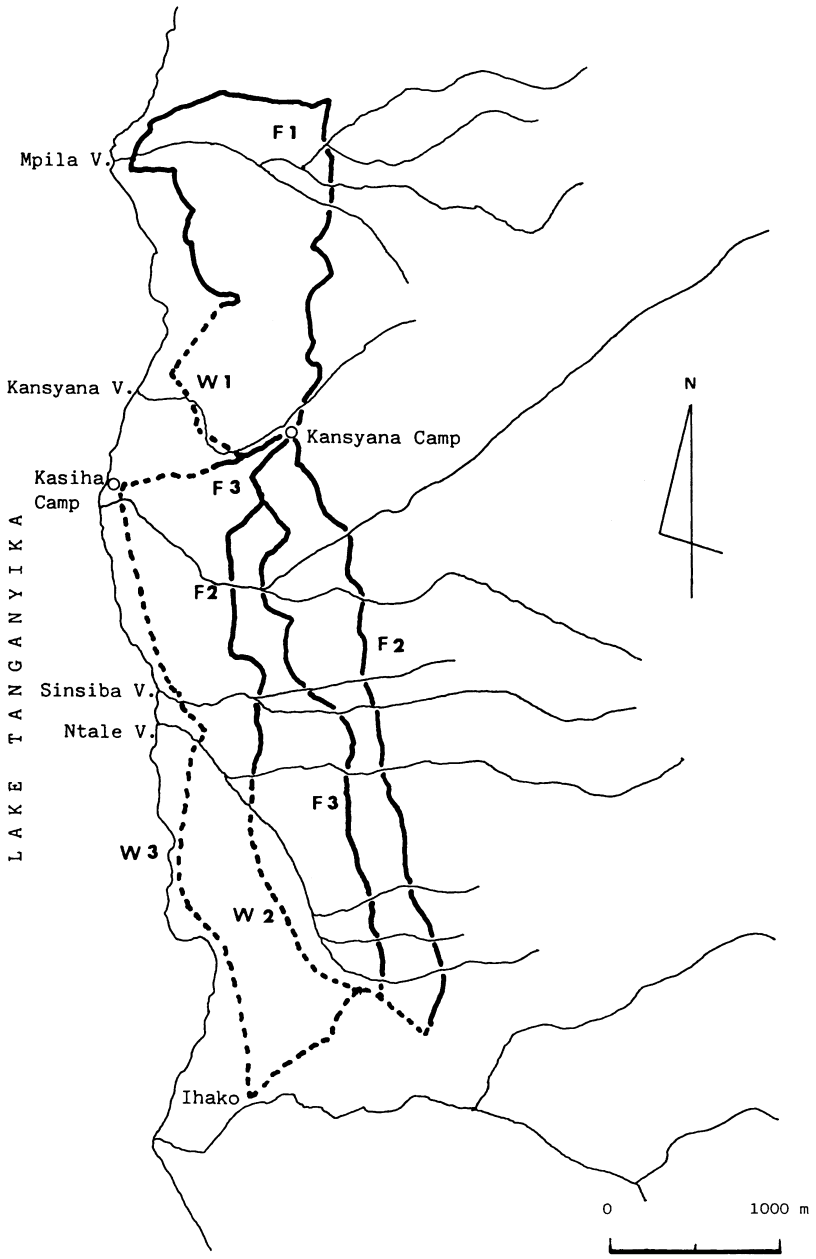

Fig. 1. The Study Area and the Three Census Routes.
(CR1: F1&W1, CR2:F2&W2, CR3:F3&W3) in 1996. CR2 and CR3 were recensused in 2000. Respective routes consist of forest (F1-F3: thick line) and woodland (W1-W3: thick dotted line). V. stands for valley. After Uehara and Ihobe (1998).

Table 1. Frequency of Encounter with Five Species of Gregarious Mammals in 1996* and 2000 (mean per day±SD).

Species	Vegetation (year)	CR2 (n)	CR3 (n)	N
Red-tailed monkey group[1)]	F (1996)	5.6±2.7 (45)	3.6±0.7 (29)	74
	F (2000)	6.5±0.87 (52)	4.3±1.39 (34)	86
	W (1996)	0.6±0.7 (5)	2.9±2.1 (23)	28
	W (2000)	0.9±0.6 (7)	3.3±1.79 (26)	33
Blue monkey group[1)]	F (1996)	0.8±0.4 (6)	0.4±0.7 (3)	9
	F (2000)	0.5±0.71 (4)	– (1)	5
	W (1996)	0	0	0
	W (2000)	0	0	0
Yellow baboon group[2)]	F (1996)	0	– (1)	1
	F (2000)	– (2)	– (2)	4
	W (1996)	– (1)	1.9±0.9 (15)	16
	W (2000)	– (2)	2.1±0.93 (17)	19
Red colobus group[3)]	F (1996)	4.5±1.9 (36)	3.3±1.0 (26)	62
	F (2000)	4.0±0.71 (32)	2.6±0.86 (21)	53
	W (1996)	0.5±0.7 (4)	0.4±0.5 (3)	7
	W (2000)	0.5±0.71 (4)	0.8±0.66 (6)	10
Warthog group[4)5)]	F (1996)	0	0	0
	F (2000)	– (1)	– (2)	3
	W (1996)	– (1)	1.6±1.5 (13)	14
	W (2000)	0.4±0.7 (3)	1.1±0.6 (9)	12

*: After Uehara and Ihobe (1998). Vegetation: F, forest; W, woodland. n: Total number of encounters in each census subunit. N: Total number of encounters. –: Frequency of encounter is not indicated, as the species was observed less than three times in each census subunit. [1)] Sample width=120 m, [2)] Sample width=180 m, [3)] Sample width=160 m, [4)] Sample width=40 m, [5)] Warthog groups include solitary animals. See Uehara and Ihobe (1998) for the census methods.

monkeys (*Cercopithecus ascanius*), blue monkeys (*C. mitis*), yellow baboons (*Papio cynocephalus*), red colobus, warthogs (*Phacochoerus aethiopicus*), bushbucks (*Tragelaphus scriptus*), blue duikers (*Cephalophus monticola*) and forest squirrels (two species combined: *Protoxerus stangeri* and *Heliosciurus rufobrachium*) (Uehara & Ihobe, 1998). Basically, the former five species are gregarious while the latter three species are non-gregarious. All species are recorded to have been consumed by M Group chimpanzees.

In 2000, the same census methods were employed by the same observer (S. U.) supported by the same Tanzanian assistant (R. Hawazi) as in 1996 (for the methods in detail, see Uehara & Ihobe, 1998). Censusing was done by recording encounters, mainly sightings, with each species within a certain sample width along each route. For the three species of terrestrial ungulates and arboreal forest squirrels, each sample width on one side of the route was taken as the perpendicular distance at which the detectability of each species declined abruptly: 20 m for warthogs and bushbucks and 10 m for blue duikers and forest squirrels. No such fall-off distance of group detectability were demarcated

within 50 m from the route for the four monkey species. Thus each sample width on one side was regarded as 50 m plus a species-typical mean radius of spatial group spread, since circles were assumed for the primate groups: 60 m for red-tailed and blue monkeys, 80 m for red colobus and 90 m for yellow baboons (Uehara & Ihobe, 1998).

For warthogs, however, group spread was omitted, as their groups were compact and small in size. Density was independently calculated only for those species observed at least three times in each census subunit or in total during the census (Uehara & Ihobe, 1998). In addition, as done in the 1996 census, solitary monkeys and individual dependent warthogs, bushbucks, blue duikers and forest squirrels were excluded from the present calculation.

Censusing was conducted eight times for each route between October and November in 2000 as in the 1996 study period, i.e., eight censuses during the late dry and early rainy seasons. Perhaps it is justifiable to conduct censuses with the same methods at several-year intervals since the subject are medium- or large-sized mammals.

RESULTS

Frequencies of encounter with the five gregarious and three non-gregarious species within the respective sample widths during the census in 2000 were respectively calculated and shown along with the corresponding data in 1996 (Tables 1 & 2). They were converted into group or individual densities (per km^2) and presented in Tables 3 and 4, respectively, along with the correspond-

Table 2. Frequency of Encounter with Three Species of Non-gregarious Mammals in 1996* and 2000 (mean per day±SD).

Species	Vegetation (year)	CR2 (n)	CR3 (n)	N
Bushbuck[1)]	F (1996)	0	0	0
	F (2000)	– (1)	– (1)	2
	W (1996)	0.5±0.7 (4)	1.9±1.8 (15)	19
	W (2000)	0	0.5±0.5(4)	4
Blue duiker[2)]	F (1996)	3.1±1.3 (25)	1.6±1.0 (13)	38
	F (2000)	5.6±2.39 (45)	3.0±1.5 (24)	69
	W (1996)	0.6±0.5 (5)	0.8±0.4 (6)	11
	W (2000)	1.3±1.09 (10)	1.5±1.73 (12)	22
Forest squirrel[2)]	F (1996)	0.4±0.7 (3)	0.9±0.8 (7)	10
	F (2000)	1.3±1.09 (10)	1.1±1.45 (9)	19
	W (1996)	– (1)	– (1)	2
	W (2000)	0	0.5±0.71(4)	4

*: After Uehara and Ihobe (1998). Vegetation: F, forest; W, woodland. n: Total number of encounters in each census subunit. N: Total number of encounters. –: Frequency of encounter is not indicated, as the species was observed less than three times in each census subunit. [1)] Sample width=40 m, [2)] Sample width=20 m. See Uehara and Ihobe (1998) for the census methods.

Table 3. Group Densities per km^2 of Five Species of Gregarious Mammals in 1996* and 2000.

Species	Vegetation (year)	CR2	CR3	Mean[1)]
Red-tailed monkey	F (1996)	6.8	6.4	6.6
	F (2000)	7.8	7.5	7.7
	W (1996)	2.4	3.9	3.5
	W (2000)	3.4	4.4	4.2
Blue monkey	F (1996)	0.9	0.7	0.8
	F (2000)	0.6	–	0.4
	W (1996)	0	0	0
	W (2000)	0	0	0
Yellow baboon	F (1996)	0	–	–
	F (2000)	–	–	0.2
	W (1996)	–	1.7	1.3
	W (2000)	–	1.9	1.6
Red colobus	F (1996)	4.0	4.3	4.1
	F (2000)	3.6	3.5	3.5
	W (1996)	1.5	0.4	0.7
	W (2000)	1.5	0.8	0.9
Warthog[2)]	F (1996)	0	0	0
	F (2000)	–	–	0.8
	W (1996)	–	6.6	5.3
	W (2000)	4.4	4.6	4.5

*: Recalculated from the data in Uehara and Ihobe (1998). Vegetation: F, forest; W, woodland.
–: Density is not calculated, as the species was observed less than three times in total or in each census subunit. [1)] Mean densities are calculated from the total number of encounters (N) in Table 1 and the area covered during the census, [2)] Warthog groups include solitary animals: see Uehara and Ihobe (1998) for the census methods.

Table 4. Individual Densities per km^2 of Three Species of Non-gregarious Mammals in 1996* and 2000.

Species	Vegetation (year)	CR2	CR3	Mean[1)]
Bushbuck[2)]	F (1996)	0	0	0
	F (2000)	–	–	–
	W (1996)	5.8	7.6	7.2
	W (2000)	0	2.0	1.5
Blue duiker[2)]	F (1996)	22.5	17.2	20.3
	F (2000)	40.5	31.7	36.9
	W (1996)	14.6	6.1	8.3
	W (2000)	29.2	12.2	16.6
Forest squirrel[2)]	F (1996)	2.7	9.2	5.4
	F (2000)	9.0	11.9	10.2
	W (1996)	–	–	–
	W (2000)	0	4.1	3.0

*: Recalculated from the data in Uehara and Ihobe (1998). Vegetation: F, forest; W, woodland.
–: Density is not calculated, as the species was observed less than three times in total or in each census subunit. [1)] Mean densities are calculated from the total number of encounters (N) in Table 2 and the area covered during the census, [2)] Excluding dependent individuals.

ing data in 1996. Note that warthog groups include solitary individuals while monkey groups do not (Uehara & Ihobe, 1998).

Daily frequencies of encounter with each species (number of groups or individuals) in the same census subunits (Tables 1 & 2) were compared between 1996 and 2000 using the Mann-Whitney *U* test. No statistically significant difference was found between the two data sets. However, the difference of encounter frequency with blue duikers in the census subunit F2 (forest vegetation for CR2) is nearly significant ($n1=n2=8$, $U=13.5$, $p \fallingdotseq 0.05$). Encounter frequencies with bushbucks were extremely low in 2000.

In 2000 I have recorded considerably larger group sizes for the two gregarious species of red-tailed monkeys and yellow baboons compared with the mean group sizes used previously (Uehara & Ihobe, 1998: Table 4). For the former species, I counted 30 independent individuals in the census subunit W3, which is more than twice as large as the mean group size estimated in 1996. For the latter, I encountered far more than 52 individuals in the same area. Moreover, more than 63 animals were observed in one group of yellow baboons in the same area in September 2000 (J. Wakibara, personal communication).

Table 5. Individual Densities per km^2 of Five Species of Gregarious Mammals in 1996* and 2000.

Species	Vegetation (year)	CR2	CR3	Mean[1)]
Red-tailed monkey	F (1996)	81.6	76.8	79.2
	F (2000)	117	112.5	115.5
	W (1996)	28.8	46.8	42
	W (2000)	51	66	63
Blue monkey	F (1996)	9	7	8
	F (2000)	6	—	4
	W (1996)	0	0	0
	W (2000)	0	0	0
Yellow baboon	F (1996)	0	—	—
	F (2000)	—	—	10
	W (1996)	—	68	52
	W (2000)	—	95	80
Red colobus	F (1996)	120	129	123
	F (2000)	108	105	105
	W (1996)	45	12	21
	W (2000)	45	24	27
Warthog[2)]	F (1996)	0	0	0
	F (2000)	—	—	1.6
	W (1996)	—	13.2	10.6
	W (2000)	8.8	9.2	9

*: Recalculated from the data in Uehara and Ihobe (1998). Vegetation: F, forest; W, woodland.
–: Density is not calculated, as the species was observed less than three times in total or in each census subunit. [1)] Mean densities are calculated from the mean group densities in Table 3 and the group sizes (see text), [2)] Excluding dependent individuals.

For the calculation of individual densities in 2000, the mean group sizes of red-tailed monkeys, 12 animals, and yellow baboons, 40 animals, estimated in 1996 (Uehara & Ihobe, 1998) seemed unrealistic. Instead, 15 for the former species and 50 for the latter were employed for convenience's sake. With respect to the other three gregarious species, however, I did not have a good opportunity in 2000 to reassess respective group sizes. Accordingly, the following figures are used again as respective group sizes for the present calculation: ten for blue monkeys, 30 for red colobus and two for warthogs (Uehara & Ihobe, 1998). Tentative estimations of individual densities of the five gregarious species in 2000 are shown in Table 5 along with the corresponding data in 1996.

In summary, although no statistically significant differences has been found, I suggest that blue duikers, red-tailed monkeys and yellow baboons may have increased and bushbucks decreased while red colobus and warthogs seem to remain rather stable in number between 1996 and 2000 (Tables 3, 4 & 5). With respect to the other two species seen infrequently in 1996, forest squirrels may not have decreased since their encounter frequencies increased twofold in 2000 (Table 2), although no such assumption could be made for blue monkeys due to their low densities in both years (Table 1).

DISCUSSION

The present results show that the population densities of the prey mammals censused again in 2000 have not decreased, with the exclusion of blue monkeys and the possible exception of bushbucks. This indicates that, excluding these two species, the predation rates as a whole including that by the chimpanzee hunting after 1995 did not exceed the population growth rates of the respective prey mammal species, although no quantitative predation data for the relevant period are available at the moment.

No conspicuous changes in group densities of the five gregarious species were recognized between 1996 and 2000. It may be, however, that individual densities of the two species, red-tailed monkeys and yellow baboons, have increased from 1996 to 2000 due to the increase in group size. More accurate data on group sizes of the gregarious mammals are needed in future studies. My observations in 2000 suggest that the mean radius of group spread for red-tailed monkeys is much longer than 10 m used in a previous calculation (Uehara & Ihobe, 1998). More accurate data on group spread are needed as well, which affect the sample widths in Table 1, and consequently the density estimations in Tables 3 and 5. It should also be pointed out that eight census days for each route during one season are insufficient for the present comparison.

At Mahale, red colobus monkeys were the most frequent prey items of the chimpanzees, followed by blue duikers between 1981 and 1995 (Uehara *et al.*, 1992; Hosaka *et al.*, 2001). Both species do not seem to have decreased

since 1996 with respect to group and individual densities (Tables 3, 4 & 5). This coincides with Ihobe and Uehara's (1999) estimate before 1996 that, in general, the chimpanzee hunting did not have a profound effect on mammalian prey populations at Mahale (annual predation rates of 1.1-3.8% for red colobus and 1.7-2.4% for blue duikers between 1981 and 1995: Boesch *et al.*, 2002). Regarding red colobus, this seems similar to the situation in Tai National Park, Côte d'Ivore (3.2-7.6%: Boesch & Boesch-Achermann, 2000) and contrasts with the results from Gombe and Kibale (Ngogo) where chimpanzee predation appears to have serious effects on red colobus populations (16-40% for Gombe and 6.5-12% for Ngogo: Goodall, 1986; Wrangham & Bergmann Riss, 1990; Stanford, 1995, 1998; Stanford *et al.*, 1994; Watts & Mitani, 2002).

Bushbucks were rarely seen in 2000 (Tables 2 & 4). Perhaps they have actually decreased in number since 1996 or even before 1996. It is worth analyzing unpublished data from Mahale of chimpanzee hunting on bushbucks after 1995, as such observations have decreased sharply since then (Mahale Mountains Chimpanzee Research Project, unpubl. data). In the past, bushbucks were regularly killed by the chimpanzees of K and M Groups. They occupied 24% of all mammalian prey (N=50) in 1966-1980 (Hosaka *et al.*, 2001). The annual offtake numbers or hunting rates of bushbucks by the chimpanzees were constant in the 1981-1990 and 1991-1995 periods: 4.3 individuals or 10.0% in the former and 4.0 individuals or 9.3% in the latter, respectively (Boesch *et al.*, 2002).

Contrary to the description by Ihobe and Uehara (1999), the estimated chimpanzee predation rates before 1996 (9.3-10%) might have been higher than the population growth rates of bushbucks. In addition, leopard predation on this species and red colobus does not seem negligible at Mahale. Although similar long-term data are not available, it may be that predation by chimpanzees and baboons (*P. anubis*) have considerably influenced the bushbuck population at Gombe (combined annual predation rates of 26.7% based on a guess of the bushbuck density for the period 1972-1981: Wrangham & Bergmann Riss, 1990).

Blue duikers were seen more often in the forest while bushbucks were observed more frequently in the woodland (Table 4). Although apparent changes in vegetation have not been observed since 1996, continuous monitoring of the increase or decrease among these two bovine species is noteworthy in relation to the secondary succession: the increase of blue duikers and the decrease of bushbucks may correspond to the seral shifts toward forest. Of course other possible factors such as infectious diseases should also be taken into consideration when we analyze the decreasing tendency of the bushbuck population within the home range of M Group chimpanzees.

Regrettably, quantitative hunting data on other large predatory animals, such as resident crowned hawk-eagles and non-resident lions (*Panthera leo*) and hunting dogs (*Lycaon pictus*) (Nishida, 1990), have never been collected. We still have a long way to go in order to understand the predator-prey relationships between various species in the Mahale ecosystem.

Finally, caution is required when using the present data for comparisons with other study sites because of the limitations, as explained previously (Uehara & Ihobe, 1998), caused by the route census methods. It is necessary to compare the results obtained by the route and the line transect methods (National Research Council, 1981; Whitesides *et al.*, 1988) in the same study area in the future in order to know if the present methods tend to overestimate or underestimate population densities of the subject species.

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Author's Name and Address: Shigeo UEHARA, *Department of Ecology and Social Behavior, Primate Research Institute, Kyoto University, Inuyama, Aichi, 484-8506, JAPAN.*
E-mail: uehara@pri.kyoto-u.ac.jp